

NOTES ON THE BEHAVIORAL ECOLOGY OF
PERRHYBRIS LYPERA (PIERIDAE) IN
NORTHEASTERN COSTA RICA

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ABSTRACT. *Perrhybris lypera* (Pieridae: Pierinae: Pierini) occurs in low adult densities in lowland tropical rain forests of Central America and northern South America. Females possess the "tiger stripe" coloration known for many classically unpalatable Neotropical butterflies and their mimics, while males resemble "whites." These differences are related to sex-limited behavioral patterns. Adult behavior, including oviposition and differences in local abundance between males and females, and certain features of juvenile behavior (larval foodplant, behavior of first instar larvae, and pupation) were studied in northeastern Costa Rica. A cluster of 18 healthy pupae of *P. lypera* was discovered on a leaf of the forest understorey tree *Ocotea* sp. (Lauraceae) and produced a 1:1 sex ratio of adults. Lengthy cluster oviposition on *Ocotea* results in bright yellow eggs being deposited in rows on the upper sides of young leaves amidst dense stellate pubescence. Prior to oviposition, considerable time is spent by the females "inspecting" the foodplant. Egg hatchability and survival for over the first three days in the wild was 100%. The egg stage lasted 16 days and the first instar larvae were gregarious. They partially devoured their egg shells and commenced communal feeding on soft leaf tissue. Adult females (presumably mated) occurred in low numbers near larval foodplants (trees), while solitary males were seldom seen. Aggregations of fresh males observed near breeding sites might have been leks, functioning to attract unmated females. Gregarious larval behavior and pupation result from cluster oviposition. They seem to facilitate aggregative behavior in male *P. lypera*.

The purpose of this paper is to report some interesting features of the behavioral ecology of adults and first instar larvae of the Neotropical pierid *Perrhybris lypera lypera* (Kollar) in northeastern Costa Rica. Perhaps owing to the small number of species of this South American genus (Seitz, 1924), and the rather secretive habits of the females in primary forest understories, little is known about the biology of *Perrhybris*. With the exception of the closely-related *P. pyr-rha* Fabricius in Brazil (Prittwitz, 1965; D'Almeida, 1921, 1922), *Perrhybris* have not been extensively studied. Virtually nothing is known about the larval foodplants of *P. lypera* and the behavior of adults and larvae. This paper is mainly observational and is not an attempt to describe the detailed morphology of the early stages of *P. lypera*.

STUDY AREAS AND METHODS

Perrhybris lypera was briefly studied during 1969 at Finca La Selva, near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica (elev. 98 m), a zone of relatively undisturbed Lowland Tropical Wet Forest (Holdridge, 1967). A collection of gregarious pupae was made from a presumed larval foodplant, and male behavior was observed.

More extensive studies of *P. lypera* were subsequently conducted at Finca La Tigra, near La Virgen de Sarapiquí (elev. 200 m) in a zone of relatively disturbed Premontane Tropical Wet Forest; these additional studies were done in February 1977, August 1977, and August 1978. These studies focused on identification of a larval foodplant, and observations of adult behavior (including oviposition), and larval behavior. Female specimens from La Selva and La Tigra match *P. lypera lypera* from Puerto Viejo, in the Allyn Museum of Entomology, as do male specimens from Guatemala and Ecuador.

At Finca La Selva, a cluster of 18 gregarious, clearly pierid pupae was found on an attached leaf of a primary forest understory tree (canopy about 4 m) and they were kept until eclosion to identify the species and sex ratio. A voucher specimen of leaves from the tree was kept for identification. On 1 February 1977, the oviposition behavior of one female *P. lypera* was studied for several hours. The eggs were collected for laboratory study a few days later. A section of the branch bearing the leaf with eggs was placed in a clear plastic bag and kept tightly sealed except for examinations. The number of eggs, their size, shape, and color were recorded; developmental time for the eggs also was estimated and the first instar larvae were examined for resting, locomotion, and feeding behavior. The study of both eggs and larvae lasted 28 days.

During the same period at Finca La Tigra, other individuals of the same tree species used by *P. lypera* for oviposition were located and the activity of adult *P. lypera* at these trees was observed. Additional voucher specimens of the leaves of these trees were collected. During later study periods (1–4 August 1977 and 3–5 August 1978), adult behavior of *P. lypera* was studied further. Of interest was the re-occurrence of adults in the same patches of forest understory for the three widely-spaced study periods at Finca La Tigra. Further observations were made on oviposition behavior by a single individual (August 1977), and inter-female interactions were noted at larval foodplant trees. The abundance and locations of males and females also were recorded.

RESULTS

Pupation Behavior and Sex Ratio

The 16 pupae produced eight females and eight males of *P. lypera*. These eclosed between 0630–0730 h. The striking sexual dimorphism of this medium-sized butterfly has been described (Seitz, 1924). Little variation between individuals of each sex was found in the adults obtained from this aggregation of pupae. The fully-sclerotized pupae

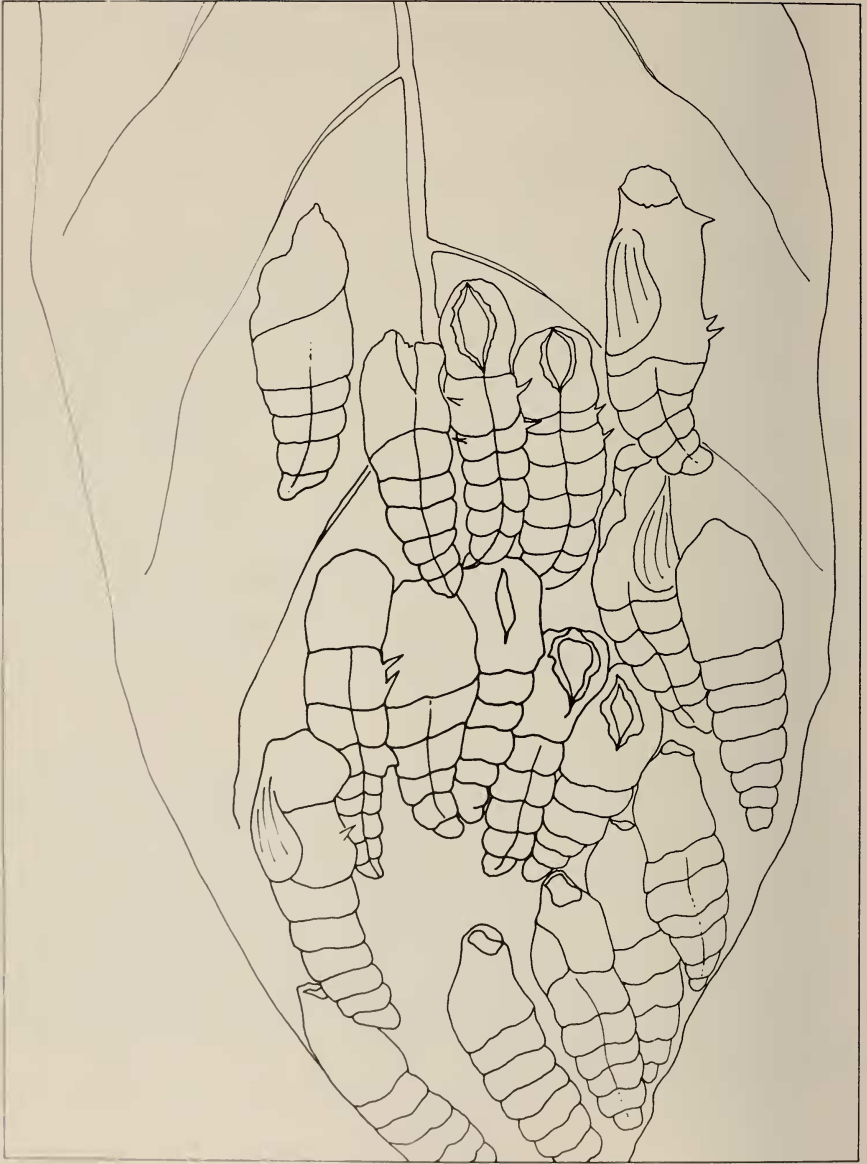


FIG. 1. An aggregation of pupae of *Perrhybris typera* on a mature leaf of *Ocotea* (Lauraceae), discovered at Finca La Selva. This drawing was made from a poor-quality black-and-white photograph of the pupal cases after eclosion.

were orange-brown. They were spaced tightly together on the underside of the distal-half of a mature leaf of *Ocotea* (Fig. 1). The pupae were positioned in an orderly fashion such that they all faced the same direction, with heads toward the leaf's petiole. The pupae were oriented upward and were inconspicuous in heavily-shaded forest understory.

Oviposition Behavior and Larval Foodplant

During the first instance of oviposition a single *P. lypera* was observed on 1 February 1977 at 1100 h. The butterfly fluttered around and through the five meter canopy of the larval foodplant (tree) for 63 min before landing on a young leaf to initiate egg-laying. The tree was in an opening within mixed advanced secondary and primary tropical rain forest. The leaves were brightly flecked with sunlight, making it possible to watch the butterfly flutter about the tree. Many light green young leaves were located near the top of the tree, clustered in threes and fours at the tip of a branch. Having alighted, the butterfly folded its wings and remained in that position until oviposition was completed [despite having a hummingbird (species unidentified) land on a nearby branch of the same tree (about 0.33 m away) and stay there for about 10 min, before flying away]. Even with binoculars, it was difficult to observe the resting butterfly from the ground, so I climbed up on some large limbs of a recently fallen tree to observe it more closely.

The butterfly remained on the leaf until 1750 h that day, indicating that oviposition lasted more than 5 hours. Periodically checking, I could just make out a raft of brilliant yellow eggs behind the butterfly. The butterfly was positioned with its head toward the leaf petiole and the raft of yellow eggs was located near the distal tip of the leaf (Fig. 2). During oviposition, the weather was intermittently sunny and overcast but these changes did not interrupt oviposition. The tree was examined each of the following three days for the presence of *P. lypera* but none was spotted. The raft of eggs was collected on the fourth day. Species determination of the tree was not possible owing to a lack of flowers and fruit. At the study site *Ocotea* is distributed as single trees (3–5 m tall), each having a dense canopy (Fig. 3). Seven trees were found within an area about 275 m², with distances between trees ranging from 20–80 m.

There were a total of 44 oblong (spindle-shaped) yellow eggs in the raft, and all but two were affixed to the young leaf in neat rows (Fig. 2). Each was securely fastened to the leaf even though the young leaf was very pubescent, a condition considerably less apparent in mature leaves of *Ocotea* (Lawrence, 1951).

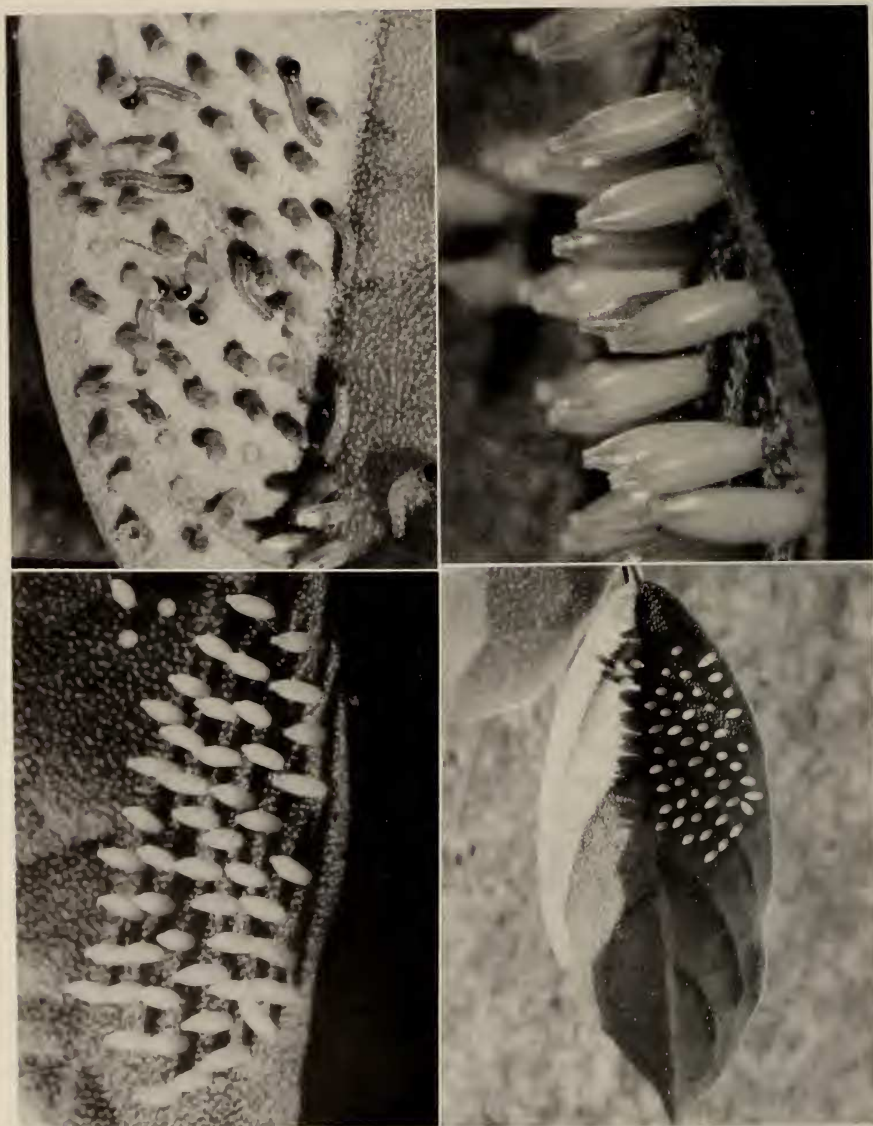


FIG. 2. Egg and larval aggregations of *P. lypera*. Clockwise from upper right: eggs on upper side of a young leaf of *Ocotea*, and first instar larvae devouring egg shells. Note that the pronounced stellate pubescence is evident in all four photographs.



FIG. 3. The canopy leaves of *Ocotea*, a tropical rain forest understory tree that is a larval food plant of *P. lypera* in northeastern Costa Rica.

Behavior of First Instar Larvae

The eggs hatched in 16 days without noticeable color changes. Hatching (Fig. 2) took place over a 26-hour period. The first instar larvae of *P. lypera* were 2.5 mm long with shiny black head capsules and striped lemon-yellow setae-covered bodies. They partially devoured their emptied egg shells. There was no cannibalism. Egg hatchability and survivorship for 3.5 days in the wild, and 12.5 subsequent days in the laboratory, was 100%. Within 2 days after hatching, the larvae became dark green and were speckled with yellow flecks. Feeding was done synchronously by the group, and was initiated at the edge of the same leaf where the larvae hatched, but on the underside. (Larvae were not reared beyond the first instar, because I had to leave the study area at this time.)

Behavior of Adults

During 16 days of observing adult *P. lypera* in the same general area a total of 28 sightings of females took place. With the exception of a second instance of oviposition (described below), these sightings consisted of seeing individual females flying through the understory,

generally 4–6 m above the ground. Two females were observed fluttering around an individual *Ocotea* about 40 m from the one where oviposition was first studied; the second tree was about the same size as the first. On this particular morning (11 August 1977) one female was observed to alight on a young leaf near the top of the tree and to imitate oviposition. Within 20 min, a second female appeared at the tree and repeatedly flew around the first female, as if attempting to land on the same leaf. A total of 7 attempted landings were made within a 10-min period. After 25 min, the second female dislodged the first one and began ovipositing on the same leaf.

While males were absent from the forest understory where females were observed, an aggregation of 12 fresh males of *P. lypera* was accidentally flushed from understory vegetation one morning (13 August 1977) about 25 m from where oviposition was first observed. No females were present. The males had been resting on a small tree. All appeared to be recently eclosed. Although considerable searching was done on several dates, solitary males were not found in the area. During April 1970 at Finca La Selva, eight groups (ranging from six to 20 adults) of freshly eclosed males were seen.

DISCUSSION AND CONCLUSIONS

Perrhybris lypera occurs in the understory of tropical rain forest in Costa Rica and is seldom seen in other habitat. The larval foodplant, *Ocotea*, is a solitary member of the forest understory. Ehrlich and Raven (1965) discuss the larval foodplant families for the Pierinae. Jorgenson (1916) mentions finding a large aggregation of larvae and pupae of *Pereute* on the trunk of *Ocotea spectabilis*. There is also one record of *Pereute* feeding on Tiliaceae (Biezanko, 1959). Both *Pereute* and *Perrhybris* belong to the Pierinae (Ehrlich, 1958) and the present discovery of *Perrhybris* feeding on *Ocotea* represents a second record for lauraceous-feeding within this subfamily and tribe. J. Röber in Seitz (1924) mentions that Brazilian *P. pyrrrha* females are found in forest habitats, while males appear to frequent various kinds of moist patches of ground. The Costa Rican observations indicate that *P. lypera* breeds in the understory layer of lowland tropical rain forests. The present-day clearance of forest habitats in northeastern Costa Rica may result in the local extinction of this species.

Males of *Perrhybris*, *Pereute*, and *Archonias* (all Pierini) exhibit gregarious behavior when imbibing moisture from the ground (Seitz, 1924); less is known about the behavioral habits of the immature stages, although Röber mentions that probably the larvae of *A. bellona* Cramer are gregarious. *Perrhybris* deposits eggs singly or in clusters on the undersides of leaves (Prittwitz, 1865; D'Almeida, 1921). Ar-

chonias tereas approximata Butler exhibits cluster oviposition and larval gregariousness in the mountains of central Costa Rica (Young, pers. obs.). Lee D. Miller (pers. comm.) pointed out that *Archonias* and *Pereute* are very closely related genera. These three genera and a few others (Seitz, 1924) exhibit gregarious behavior generally not seen in other genera of the Pierini. For example, the Neotropical *Itaballia* (Pierini) and *Dismorphia* (Dismorphinae) exhibit single oviposition, even though a female may deposit several eggs on the same individual foodplant during one visit (Young, 1972a, b). In *Perrhybris*, gregarious behavior is evident in the larvae and pupae, a consequence of cluster oviposition. Adults of either sex also may be gregarious. Gregariousness of larvae is well known in several other pierid genera, although the evolutionary origin of this behavior is unknown.

Most aposematically-colored insects are equipped with powerful chemical defenses. They often form conspicuous aggregations of individuals (Cott, 1957). Vertebrate predators quickly learn to avoid them, presumably because of the vivid coloration which is reinforced by the gregarious behavior (Brower & Brower, 1964; Eisner, 1970). In some species of *Nymphalis* (Nymphalidae) with gregarious larvae, solitary larvae are discovered and are eaten more quickly than individuals in groups (Mosebach-Pukowski, 1937). In *Perrhybris*, the gregarious habits of larvae and pupae are probably protective, as well. The leaves of *Ocotea* contain highly odorous oils, in addition to a myristic aldehyde and a sesquiterpene (Uphof, 1925). These secondary compounds become effective chemical defenses in some insects (Eisner, 1970), and they are sometimes obtained from foodplants (Eisner & Meinwald, 1965). The gregarious yellow and green speckled larvae and aggregated reddish-orange pupae suggest aposematic coloration and behavior, as does the coloration of the adult females. The closely related *P. pyrrha* is considered a classic example of sex-limited Batesian mimicry, yet the information reported here for *P. lypera* suggests that these butterflies are unpalatable. The crucial evidence, namely the ability of the larvae to sequester noxious secondary compounds, is lacking and warrants study. The problem becomes complex when a species feeds on more than one foodplant, since lepidopteran larvae can switch between palatable and unpalatable properties depending upon the foodplant (Rothschild et al., 1979). The vivid yellow aggregated eggs of *P. lypera* are not mimicking any extrafloral nectaries of *Ocotea*, as are the eggs of some species of *Heliconius* butterflies (Nymphalidae: Heliconiinae) on their larval foodplants, Passifloraceae (Benson et al., 1976), but perhaps they are protected from egg predators such as ants, by being positioned in a dense matting of

stellate pubescence on young leaves. As seen for *Mechanitis* (Nymphalidae: Ithomiinae) (Young & Moffett, 1979), such egg clusters may be so protected before group related chemical defenses arise in the larval stage.

Perrhybris lypera exhibits considerable oviposition site-selection. The relatively long period of surveying the larval foodplant before laying eggs, the selection of young leaves for egg-laying, and the apparent displacement behavior of one ovipositing female by another female indicate a highly selective or specialized form of oviposition. Butterflies and other insects that deposit large quantities of eggs on a single leaf may exhibit such behavior as an adaptive response to insuring the survival of their progeny. However, such behavior may have certain advantages for the female butterfly herself. The sedentary behavior associated with the slow and careful deposition of many eggs at a single spot in the environment could be considered as a "low risk" activity for the female (Maynard Smith, 1978), in that the stationary insect is concealed from predators which might otherwise eat it before the eggs are deposited. Even aposematically-colored butterflies are eaten by predators such as birds (Calvert et al., 1979). Such behavior may be most adaptive for butterfly species with restricted daily activity. *Perrhybris* females are found in the same patch of forest understory over long periods, suggesting that mated females tend to stay near foodplants. If larval foodplant patches are relatively scarce over extensive areas of habitat, this could be an additional factor selecting for cluster oviposition.

The preciseness of selecting young leaves of *Ocotea* probably allows the young larvae to feed successfully on soft tissues. In some *Papilio* (Papilionidae) females can distinguish young and old leaves of the foodplant based on color differences in the leaves (Vaidya, 1969). The stellate pubescence of the leaves is not a deterrent to egg deposition or feeding of young larvae. In another plant-herbivore interaction, namely *Mechanitis isthmia* and various Solanaceae with dense coverings of stellate pubescence on leaves, communal feeding in the first and second instar larvae facilitates the breaking down and removal of the pubescence, which would otherwise be difficult for solitary larvae to penetrate (Young & Moffett, 1979). Communal feeding in the gregarious larvae of *P. lypera* may serve a similar function. Further detailed field studies are needed to determine the parameters of synchronous group activities in the larvae, such as resting, feeding, molting, and pupation.

The presence of female *P. lypera* at the same site at different times of the year indicates that breeding is probably continuous throughout the year, even though the region experiences a slight "veranillo" dur-

ing January and February. Understory habitats may be insulated to some degree from seasonal changes in rainfall. Ebert (1969) found that adult *Pereute antodyca* (Boisduval) and *P. swainsoni* (Gray) in highland rain forest in eastern Brazil are active throughout most of the year. In northeastern Costa Rica *Perrhybris* female densities in areas of forest where the larval foodplants occur are generally low (from 1–5 individuals are seen on a given day at one area). The absence of a similar distribution of males is behavioral, since egg clusters produce a 1:1 sex ratio, assuming that the pupal data are typical for a population.

Synchronous eclosion of both sexes in a cluster of pupae permits mating to take place quickly, and, once completed, females disperse in search of oviposition sites. Such male aggregations are different from the well known cases of male pierids aggregating at mud puddles. Freshly-eclosed *Perrhybris* males aggregate on forest understory plants where they are not engaged in feeding. Perhaps such aggregations function to facilitate courtship in a manner analogous to the well-documented cases of lek behavior in some vertebrates (e.g., Downhower & Armitage, 1971). Further studies are needed to examine the function of male aggregations in *Perrhybris*, their locations in relation to preparation sites, and the prediction that recently-mated females rapidly disperse from places of high male density as they search for larval foodplants with patchy distributions. Under such a breeding system, the striking sexual dimorphism in wing coloration in *P. lypera* may accomplish several functions: in addition to reinforcing a warning of female unpalatability, and possible mimetic confusion for vertebrate predators, it may facilitate recognition of sex in the shaded forest understory where aggregations of males may serve as "whiteflags" for attracting unmated females.

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NOTES ON THE TYPE AND TYPE COLLECTOR OF
PARNASSIUS BEHRII (PAPILIONIDAE)

Parnassius behrii was described by W. H. Edwards (1870, Trans. Amer. Entomol. Soc. 3: 11) from a California specimen that he had received from H. H. Behr. In his treatment of the types of butterflies named by W. H. Edwards, F. M. Brown (1975, Trans. Amer. Entomol. Soc. 101: 1-31) gives the type locality of *Parnassius behrii* as "near the summit of Mt. Lyell, Yosemite Valley, California" and cites J. W. [sic M.] Hutchings as the collector. Brown relied on Henry Edwards (1878, Proc. Cal. Acad. Sci. 11-14) for this information. On p. 12 Edwards stated that "*P. behrii* was taken by Mr. J. W. [sic] Hutchings, formerly of Yosemite Valley, near the top of Mt. Lyell, at an altitude of nearly 11,000 ft." On p. 13, he further relates that the type of *behrii* was taken by Mr. Hutchings.

This information is in error. J. M. Hutchings could not have collected the types of *P. behrii* on Mount Lyell. Hutchings (see accompanying note, J. Lepid. Soc. 34: 68) lived in Yosemite Valley from 1862 until 1902. He reported on his climb of Mount Lyell in his book (Hutchings, 1886, In the Heart of the Sierras, priv. publ.), and while he does not give the dates of his climb, he states that the climb was inspired by John Muir's report of a "live glacier" on Mount Lyell. He further states that he found the card of a Mr. Tileston on the summit some ten days after it had been left. This information is a bit conflicting as Muir (1872, Overland Monthly, Dec.) indicated that he discovered the glacier in October 1871. Tileston (1922, Letters of John Boies Tileston, Boston, privately printed) wrote that he reached the summit "on Monday the 28th August, 1871." Possibly Hutchings mistook the date on Tileston's card, but in either case, he did not make the climb before late in the summer of 1871 and even more likely before the summer of 1872. Edwards had described *Parnassius behrii* in January or February of 1870.

While Hutchings could have collected the types of *P. behrii*, he could not have collected them on Mt. Lyell. He undoubtedly did, however, collect the specimens that came into the hands of Henry Edwards. It is much more likely that the types of *P. behrii* were collected by members of the California State Geological Survey, who supplied Behr with most of his "High Sierra" materials, during the summers of 1863 or 1864. W. H. Brewer and C. F. Hoffman, of the Survey, were the first to climb Mount Lyell, the mountain which they discovered and named, on 2 July 1863.

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